

ADAPTIVE SIGNIFICANCE OF SHELL TORSION IN MYTILID BIVALVES

by ENRICO SAVAZZI

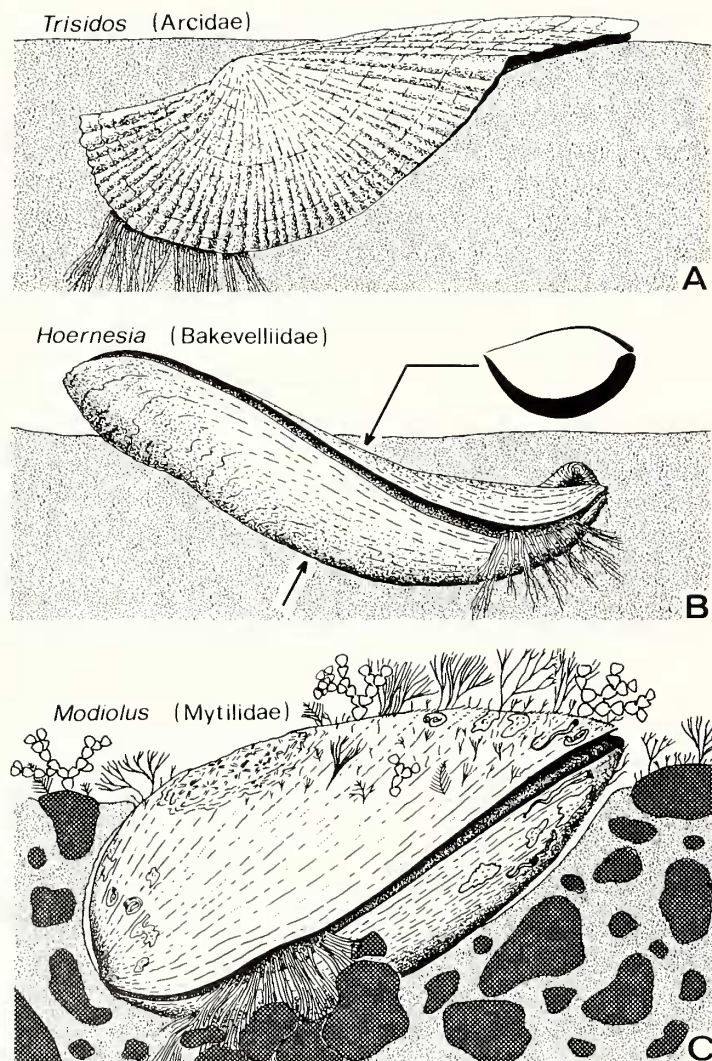
ABSTRACT. A twisted commissure plane is a common feature in several species of the mytilid genus *Modiolus*. Observations on a semi-infaunal population of *M. americanus* in Bermuda suggests that the twisted shell morphology maximizes the length of posterior commissure raised above the sediment surface while keeping its profile low, with minimum risk of accidental damage. Thus, the shell morphology in the twisted Mytilidae represents adaptive convergence with the twisted Arcidae and Bakevelliidae. In these two families, however, the torsional direction is genetically fixed, while in the Mytilidae both the direction and the amount of torsion seem to develop as a phenotypic response to the shell orientation relative to the substrate.

SEVERAL infaunal or semi-infaunal representatives of the bivalve families Arcidae and Bakevelliidae possess a twisted commissure plane (McGhee 1978; Savazzi 1981). The twisted Arcidae (*Trisidos* and at least one species of *Barbatia*) are typically endobyssate soft-bottom dwellers, although some of the less-twisted species can live facultatively as epibyssate dwellers on solid substrates (McGhee 1978; Savazzi 1981). *Trisidos* is a sluggish burrower (Tevesz and Carter 1979). The twisted commissure lifts the posterior region of the shell above the surface of the sediment and aligns it roughly horizontally (text-fig. 1A). This allows the inhalant and exhalant mantle regions to be widely spaced (McGhee 1978). The twisted Bakevelliidae (*Hoernesia*, *Gervillia*) were similarly soft-bottom dwellers. They are not likely to have been active burrowers, and lived partly buried in the sediment resting on one valve. The anchoring function of the byssus was supplemented by selective thickening of the lowermost valve (with the possible exception of the Cretaceous *Pseudoptera*). This adaptation facilitated passive re-orientation of the organism by waves or water currents after accidental disturbance of the life position (text-fig. 1B). Shell torsion offers the additional advantage that the posterior commissure, emerging from the sediment roughly horizontally, offers less resistance to water currents and is less likely to be accidentally damaged by objects rolling on the bottom (McGhee 1978; Savazzi 1981).

The torsional direction is defined as the direction of twisting of the proximal part of the shell with respect to the distal one, orienting the shell with the hinge parallel to the line of sight. Both clockwise and counter-clockwise torsion is known to occur in the Arcidae and Bakevelliidae (McGhee 1978; Savazzi 1981 and unpublished data). In all instances, however, the torsional direction is constant at the generic or specific level, and therefore appears to be genetically fixed. Evidence suggests that the twisted shell morphology evolved repeatedly within both families. It is therefore reasonable to expect that shell torsion also evolved convergently in other similarly pre-adapted bivalve groups. Further examples of shell torsion in different taxonomic groups would provide an opportunity for indirectly checking the ideas on the adaptive value and evolution of the twisted-shell morphology in the Arcidae and Bakevelliidae (cf. Savazzi 1983).

Infaunal representatives of the Mytilidae are the most likely candidates for this search, since they have life habits comparable with those of the twisted Arcidae and Bakevelliidae and, lacking siphons, they similarly need to leave a consistent length of the posterior commissure exposed above the surface of the sediment, in order to avoid fouling by sediment particles and mixing of the inhalant and exhalant currents. In addition, since the Mytilidae belong to the superfamily Pteriomorphia together with the Arcidae and Bakevelliidae, they possess relatively close anatomical affinities. In fact, a survey of Recent mytilids showed that several species of *Modiolus* are often noticeably twisted about the hinge axis in a manner closely comparable with the twisted Arcidae. Singularly enough, no

mention of shell torsion was found in the literature on these species. A number of other mytilid species often display a wavy or otherwise irregular commissure. Although these irregularities do result in a non-planar commissure, they do not conform to the definition of shell torsion (McGhee 1978) and are therefore excluded from the present discussion. Since the twisting in *Modiolus* is always greatest between the antero-ventral and the posterior shell regions, as in the twisted Arcidae and Bakevelliidae, it seemed possible that the shell torsion could be similarly adaptive. However, the degree of twisting turns out to be extremely variable within a single species, and only some of the individuals display torsion at all. Furthermore, it was found that both clockwise and counter-clockwise torsion normally occur side by side within the same species. It was therefore felt that the functional interpretation of the twisted-shell morphology would remain questionable in this specific case, unless direct observations could be carried out on twisted mytilids in their natural environment.



TEXT-FIG. 1. Schematic illustration of twisted bivalves in life position. A, *Trisidos yongei* Iredale, Recent, East Indies. B, *Hoernesia socialis* (Schlotheim), Middle Triassic, southern West Germany. The transverse section shows the characteristic thickening of the lowermost valve. C, *Modiolus americanus* Leach, Recent, Bermuda.

MATERIAL AND METHODS

Modiolus americanus Leach, one of the mytilids exhibiting shell torsion, is a large species living in the West Indies. Stanley (1970) described it as occurring in clear sand or in subtidal grass flats, mostly or totally buried in the sediment and byssally attached to the roots of seaweeds or to coarse sediment particles. The writer located a population of this species living at a depth of 1–2 m along the south-eastern coast of Harrington Sound, Bermuda, in August 1982. The bivalves were living in coarse, muddy sand mixed with sandstone pebbles deriving from a nearby overhanging rocky cliff. The thick byssus was always found to be anchored to a fairly large amount of coarse sediment particles, requiring considerable physical effort to dislodge the shell. Roughly one-third of the shell surface was exposed and heavily overgrown by algae and encrusting organisms. The life position was initially recorded by marking the exposed parts before dislodging the shell, but it was subsequently found that the distribution of epibionts is a fairly reliable indicator of the exposed shell regions. Only thirty-one individuals could be located, since their distribution was patchy, and the sediment type rapidly changed to barren muddy sand, unsuitable for *M. americanus*, a few metres away. Dead shells and isolated live individuals were collected elsewhere in Bermuda, but no other population was found. A total of forty-one individuals was observed in the living position.

The angle of shell torsion was measured by projection on to a plane perpendicular to the hinge axis. The inclination of the posterior commissure relative to the surface of the sediment could not be reliably measured because of irregularities in the substrate. For most individuals, it was estimated at 30° to 60°. Only two individuals were found lying with the commissure plane approximately vertical.

RESULTS

The data relative to live *M. americanus* (text-fig. 2A) show an almost perfect association between the direction of shell torsion and the lateral inclination of the commissure plane in the living position. With a single exception, possibly due to a previous disturbance, the direction of shell torsion is such as to maximize the length of posterior commissure raised above the surface of the sediment, as found in other twisted bivalves (text-fig. 1C). Lateral asymmetries (other than twisting about the hinge axis) were not noticed in the anatomy of the soft parts, nor in the distribution of the periostracal hairs on the outer surface of the shell. The two specimens with a vertically oriented commissure showed negligible torsion. Otherwise, the lack of information on inclination of the commissure relative to the substrate precludes detection of any correlation between torsional angle and obliquity of shell insertion in the sediment.

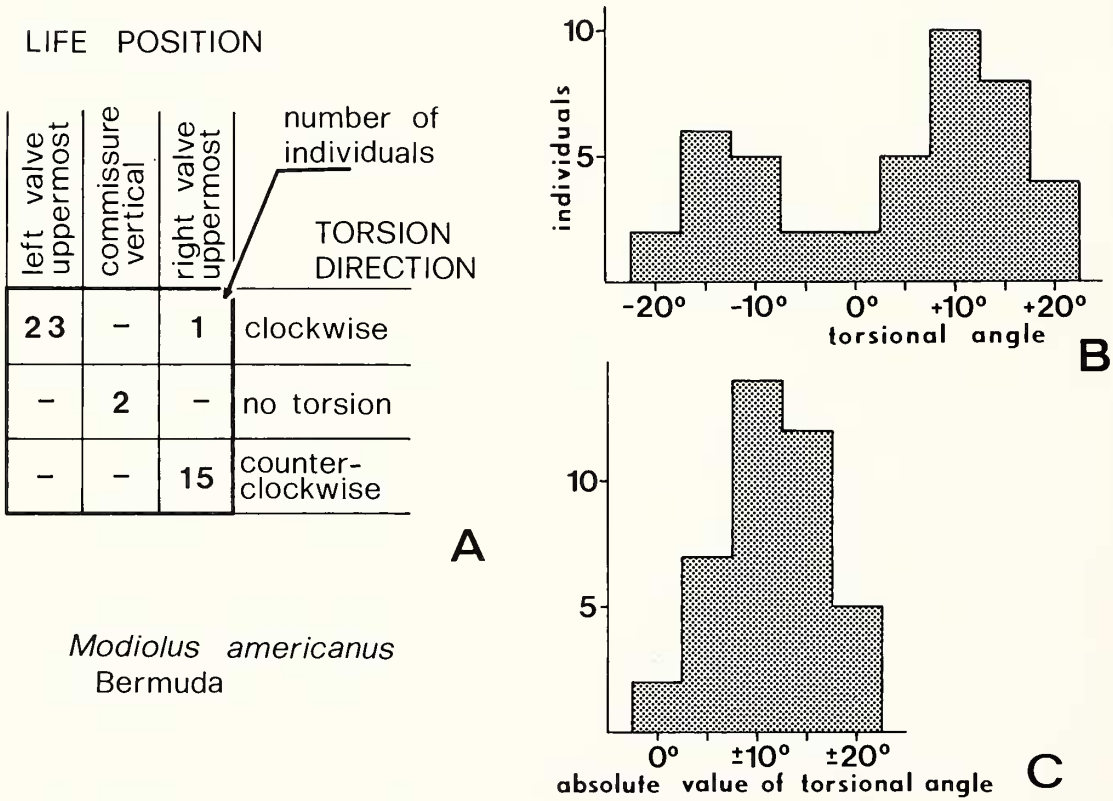
The histogram in text-fig. 2B shows the degree of twisting of the commissure plane for the living individuals of *M. americanus* collected for this study. The torsional angle of counter-clockwise twisted individuals is arbitrarily given a negative sign. When the absolute value of the torsional angle is displayed, the distribution becomes unimodal (text-fig. 2C). Together with the comparable number of clockwise and counter-clockwise twisted individuals, this suggests that the direction of shell torsion is determined by a stochastic process.

The bimodal distribution in text-fig. 2B contrasts with those obtained from dead shells of *M. americanus* and other Recent species from museum collections (text-fig. 3). This discrepancy can be explained by the fact that species in museum collections are usually represented by several shell-lots from different localities and environments. According to the functional interpretation of shell torsion as a facultative adaptation to life in soft sediments, the twisted-shell morphology should be expected to occur only in populations living infaunally or semi-infaunally. *M. americanus*, for instance, occurs as an epibyssate dweller on rocky bottoms in North Carolina (Van Dover and Kirby-Smith 1979). In such a case, shell torsion would not be expected. Environmental data are usually absent in museum material, so that the above hypothesis cannot be tested. None the less, it is interesting to note that the percentage of twisted individuals in museum collections was found to be extremely variable among shell-lots of the same species but from different localities.

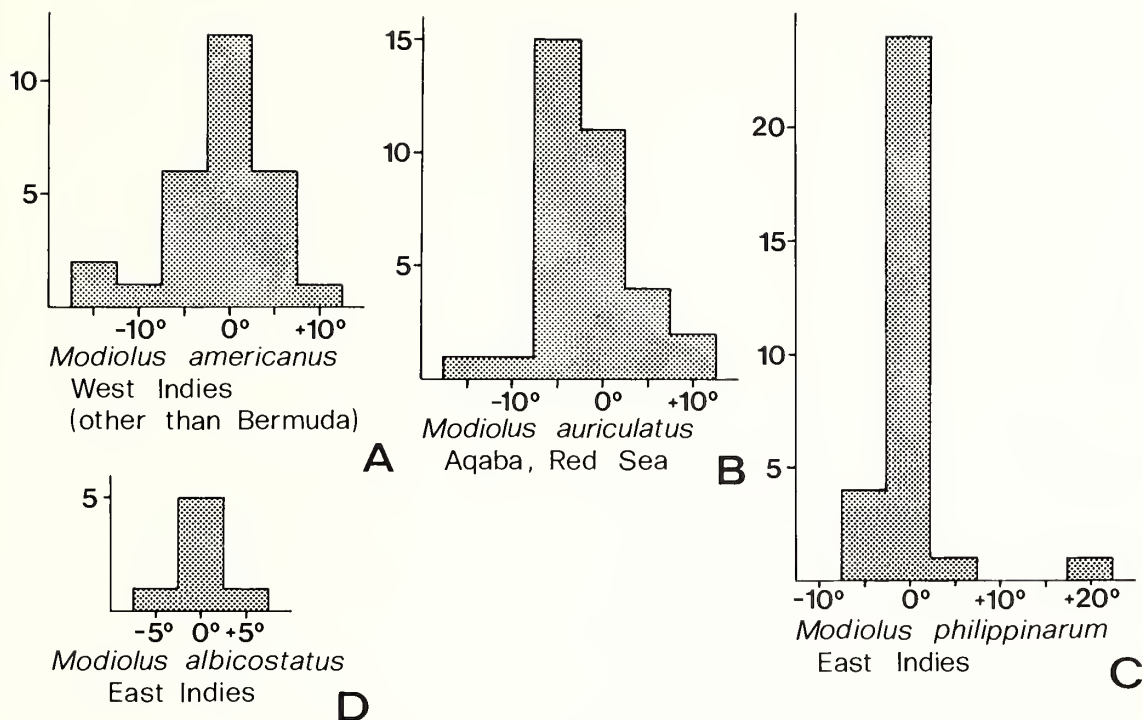
DISCUSSION

The relatively small number of individuals of *M. americanus* and the other twisted mytilids available for this study does not allow an effective statistical treatment. However, the approximately equal number of clockwise and counter-clockwise twisted individuals (with the exception of *M. auriculatus*, which is represented by a beach collecting and could therefore be biased by sorting) suggests that the direction of shell torsion in *Modiolus* is not genetically determined, but rather develops as a phenotypic response to the shell orientation relative to the substrate. The twisted Arcidae and Bakevelliidae are usually found in loose, essentially homogeneous sediments. The correct life orientation can be assumed by the settling veliger and/or be subsequently established by active or passive means. Therefore, a genetically fixed direction of torsion does not decrease the adaptiveness of the organism. A fixed torsional direction probably simplifies the introduction of other coadaptive inequivalve characters (differential valve weighting in the Bakevelliidae, different valve overlap in the Arcidae, functional inequivalve shell sculpture in representatives of both families: McGhee 1978; Savazzi 1981) in the morphogenetic programme of the shell.

M. americanus as observed during the present study, on the other hand, is better described as a byssally anchored semi-infaunal nestler among sediment-covered pebbles, rather than as a true soft-sediment dweller. The local topography of the substrate, rather than a preference of the veliger, seems



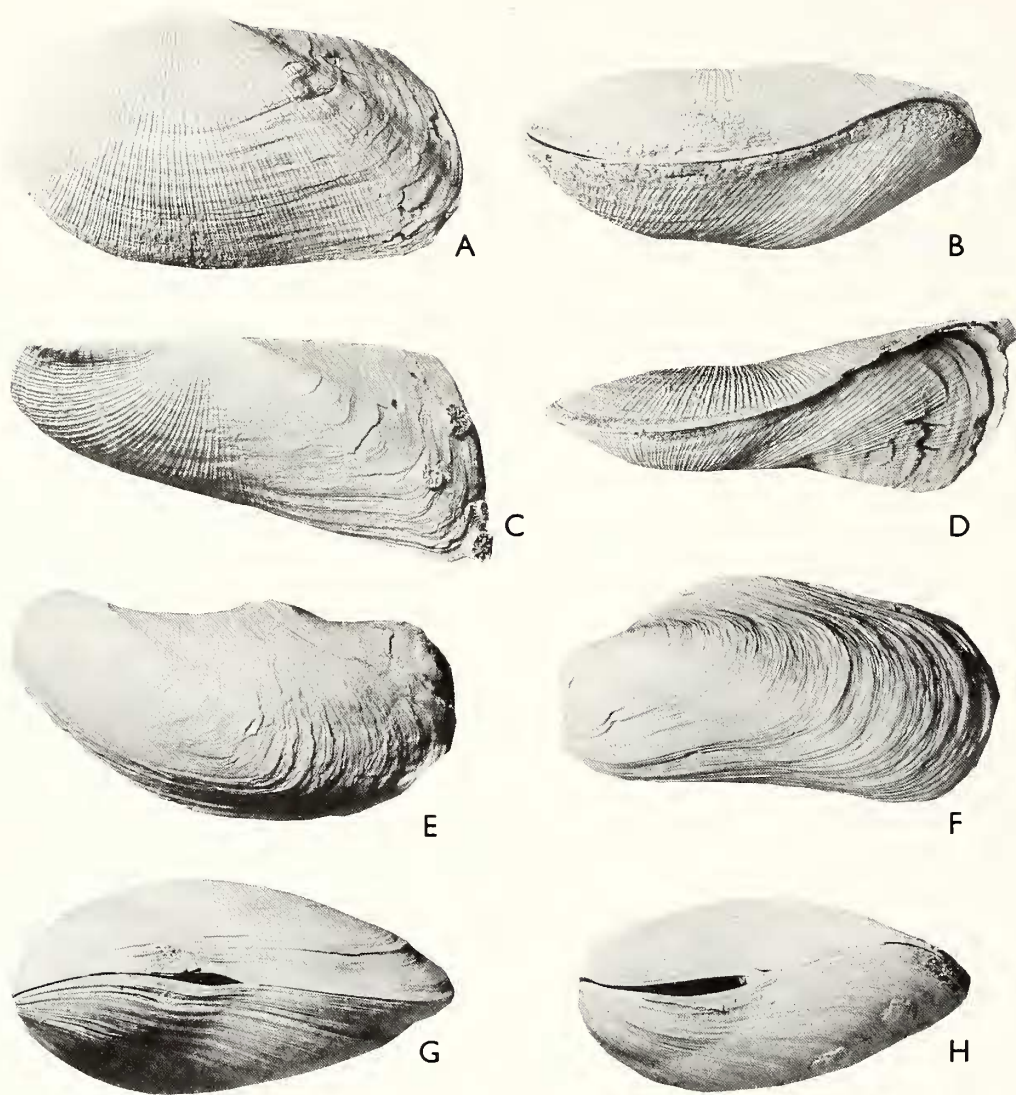
TEXT-FIG. 2. Occurrence of shell torsion in *Modiolus americanus* from Bermuda. A, relationship between life position and direction of shell torsion. B, distribution of the amount of shell torsion. Counter-clockwise and clockwise torsion are given negative and positive values, respectively. C, distribution of the absolute value of the amount of shell torsion.



TEXT-FIG. 3. Occurrence of shell torsion in Recent mytilid species. See preceding figure for explanation.

to be the most likely factor determining which valve will happen to lie uppermost. The possibility of developing either direction of torsion would therefore considerably increase the adaptiveness of the organism and, since apparently not associated with other inequivalve characters, it would not require a particularly complex morphogenetic programme. The alternative hypothesis, i.e. that the direction of torsion is genetically fixed and that the organisms assume a life position compatible with the anticipated torsion direction, would require a considerably more complex morphogenetic and behavioural programme. Since the possible shell orientation is highly constrained by the substrate morphology, only a proportion of the settling veligers would be in the condition of taking advantage of the shell twisting.

Other characters indicate that the adaptive strategy of *M. americanus* is rather different from that of both twisted Bakevelliidae and Arcidae. In these two families, the torsional angle reaches its maximum value between the posterior commissure line and the byssal gape. In *M. americanus* and in other twisted mytilids, on the other hand, the maximum torsional angle, relative to the posterior commissure, is often found slightly anterior to the byssal gape. When *M. americanus* is feeding normally, the shell gapes all around, and the long and slender pedal retractor muscles are contracted, pulling the byssus anteriorly. As a result, the shell is pushed backwards and upwards about half a centimetre, thus elevating the posterior commissure clear of the sediment surface and the surrounding algae. The torsion in the shell region anterior to the byssal gape causes the shell to rotate slightly as it is pushed backwards, further elevating the posterior commissure. When the mollusc adopts the feeding position, a cavity forms between the buried shell surfaces and the surrounding sediment, allowing the growth of interstitial cemented epibionts on the shell (text-fig. 1c). Since the shell surfaces exposed above the substratum are heavily overgrown by algae, the encrusting red algae



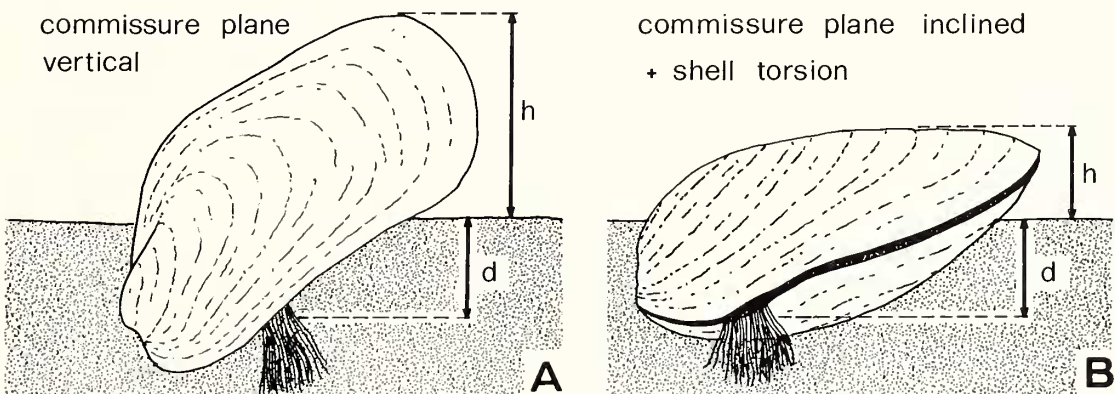
TEXT-FIG. 4. Twisted bivalves. A-B, *Trisidos semitorta* (Lamarck), Recent, Philippines; left lateral and ventral views, $\times 0.75$, NRS (NRS = Naturhistoriska Riksmuseet Stockholm). C-D, *Tr. tortuosa* (Linnaeus), Recent Philippines; left lateral and ventral views, $\times 0.75$, NRS. Note the corals attached to the posterior region of the left valve, which is exposed in life position (compare with text-fig. 1A). E, *Hoernesia socialis* (Schlotheim), Middle Triassic, Württemberg (West Germany); left lateral view, $\times 1.5$, Paleontologiska Institutionen Uppsala. F-G, *Modiolus americanus* Leach, Recent, Bermuda; left lateral and ventral views, $\times 0.75$. H, *M. philippinarum*, Recent, Bali; ventral view, $\times 2$, NRS. Note that the specimens in G and H are counter-clockwise and clockwise twisted, respectively.

and worm tubes are often more frequently found on the buried shell regions, where they face little spatial competition. In other twisted mytilids, in contrast, the exposed parts are more heavily overgrown by calcareous algae than the buried parts. Therefore, the distribution of cemented epibionts would be of little use as an indicator of the life habits of fossil mytilids.

Repaired minor damage to the posterior commissure is a common feature in the twisted Arcidae and Bakevelliidae and in most twisted *Modiolus* (text-fig. 4). Such damage is probably the result of the impact of objects rolled on the sea floor by waves or water currents. Traces clearly referable to the attack by shell-chipping predators are uncommon. In the twisted Arcidae and Bakevelliidae, the anterior and ventral commissure is generally immune from damage, since these parts are buried. In *M. americanus*, on the other hand, repaired damage to the shell margin is often also observed in the byssal region (text-fig. 4F). This is explained by the fact that *Modiolus*, unlike the other twisted bivalves, is byssally attached to, and surrounded by, buried rock fragments. When the posterior end of the shell is moved, the shell surface exerts a leverage against these solid bodies, the byssus acting as a fulcrum. A closely similar breakage pattern is often observed in epibyssate bivalves (e.g. *Mytilus*, *Arca*). Thus, it may be difficult to infer the life habits of fossil *Modiolus* from either the distribution of epibionts or the patterns of repaired marginal fractures. Shell torsion, on the other hand, is an easily recognizable feature and therefore a useful tool in autecological analysis, since it should be expected to occur only in those individuals living semi-infaunally and lying on one valve. As shown by the records in the literature, the life habits of single species can vary in different localities, resulting in a variable percentage of twisted individuals.

It was not possible to assess the frequency of occurrence of shell torsion in fossil mytilids. However, a late Caenozoic mould of a *Modiolus* species from the West Indies, closely related to *M. americanus* (Paleontologiska Institutionen Uppsala Nr. 1b 6007) shows pronounced shell twisting.

The principal adaptive advantages of shell torsion in the Arcidae and Bakevelliidae, i.e. leaving a suitable length of the posterior commissure clear of the sediment, to facilitate the respiratory and feeding current exchanges, and aligning it approximately horizontally, so that it would be less likely to be accidentally damaged (McGhee 1978; Savazzi 1981), apply to the twisted Mytilidae as well. The frequency of repaired damage to the posterior commissure in all twisted bivalves attests to the vulnerability of this exposed shell region. Other bivalves living in similar environments with part or all of the commissure exposed rely on several protective mechanisms. The shell margins are very thick



TEXT-FIG. 5. An idealized comparison of life positions with the commissure plane vertical (A) and inclined (B) shows that the latter reduces the height of the portion of the shell projecting above the surface of the substratum (h). The length of exposed posterior commissure is the same in both cases. Shell torsion coupled with a reclining position on one side (B) allows the byssus to be buried at a suitable depth within the substratum (d) to provide firm anchorage.

(e.g. epibyssate arks; some oysters), or the mollusc relies on extensive repair capabilities (e.g. *Pinna*; Yonge 1953). Alternatively, thick periostracal bristles or flexible and frilled shell margins may act as elastic shock absorbers (*Pteria*, *Isognomon*, some mytilids). Text-fig. 5 shows how shell torsion in *Modiolus* significantly reduces the height and vulnerability of the parts of the shell projecting above the surface of the sediment, while at the same time it allows the byssus to be buried at a suitable depth to ensure a reliable anchorage. A nearly horizontal posterior commissure, moreover, allows feeding on the particle-rich bottom layer of water.

According to McGhee (1978), evolution of the twisted morphology in the Arcidae and Bakevelliidae was rendered possible when a morphogenetic programme supplemented or substituted the interference of the byssus with the mantle margins in determining the shape of the byssal gape. The byssal gape is a weakly controlled region of the shell also in the Mytilidae, as shown by its greatly variable shape and extension. Therefore, McGhee's explanation can be applied to this family as well.

CONCLUSIONS

The twisted-shell morphology in *Modiolus* represents an adaptation to a semi-infaunal life habit with the commissure plane lying on one side, and constitutes therefore a functional convergence with the twisted Arcidae and Bakevelliidae. While the potential for shell torsion is present in several species of *Modiolus*, its expression is dependent upon life habits and environmental conditions. It is significant that shell torsion in *Modiolus* was observed solely in species possessing a relatively unspecialized shell shape. Very streamlined and elongated species, adapted to burrowing at a high angle to the sediment surface, and *Mytilus*-like species with a broad flat ventral region, suitable for epibyssate attachment, were never found to be twisted. Similarly, shell torsion was not found in the mytilinid genus *Brachidontes*, whose infaunal representatives burrow at a high angle to the sediment surface (Stanley 1970).

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